

The MN System: Regional Or Continental?

JOHN ALROY¹, RAYMOND L. BERNOR^{1,2}, MIKAEL FORTELIUS³ & LARS WERDELIN⁴

With 5 figures

Abstract

In this paper we apply disjunct distribution ordination (DDO) to a large set of Miocene to Pleistocene mammal localities from western Eurasia. This multivariate method creates a sequence of taxonomic first and last appearance events that minimizes the number of age-range overlaps. Our aim is to compare the event sequence with the existing Eurasian MN system of mammalian biochronology. Our results show that: 1) the sequence and the MN system ordination of localities are highly correlated; 2) a combined data set of western and eastern localities performs better in this regard than either data set separately; 3) most disagreements between the methods involve faunal lists of inadequate length. These results confirm that the current MN system is robust and suggest that it can be usefully extended to encompass all of Eurasia. Specifically, we expect Eurasian mammal biochronology to be refined through the use of algorithmic techniques such as DDO, which are likely to provide objectivity and quantification without generating unpredictable results.

Kurzfassung

In dieser Arbeit wird die Methode der „disjunct distribution ordination“ (DDO) auf eine große Menge von miozänen bis pleistozänen Säugetierlokalitäten West-Eurasiens angewendet. Diese multivariate Methode erzeugt eine Abfolge von „first appearance“ und „last appearance events“ taxonomischer Einheiten, die die Zahl von Überlappungen der Zeitbereiche minimiert. Es ist dabei unser Ziel, diese Event-Abfolge mit dem existierenden Eurasischen MN-System der Säugetier-Biochronologie zu vergleichen. Unsere Ergebnisse zeigen, daß 1) die Einstufung von Lokalitäten in die Abfolge der Events und in das MN-System stark korreliert sind, 2) ein kombinierter Datensatz mit westlichen und östlichen Lokalitäten in dieser Hinsicht bessere Ergebnisse liefert als jeder der getrennten Datensätze und 3) die meisten Unstimmigkeiten zwischen den Systemen auf Faunenlisten von unzureichender Länge zurückgehen. Diese Ergebnisse bestätigen, daß das gegenwärtige MN-System stabil ist und lassen vermuten, daß seine Ausdehnung auf das gesamte Gebiet Eurasiens sinnvoll ist.

1 Department of Paleobiology, Smithsonian Institution, Washington, D. C. 20550, USA.

2 College of Medicine, Department of Anatomy, Laboratory of Evolutionary Biology, Howard University, Washington, D. C. 20059, USA.

3 Department of Geology, University of Helsinki, P. O. Box 11, SF-00014 University of Helsinki, Finland.

4 Department of Palaeozoology, Swedish Museum of Natural History, Box 50007, S-104 05 Stockholm, Sweden.

Insbesondere erwarten wir, daß die Biochronologie Eurasiens durch die Anwendung algorithmischer Techniken wie DDO verfeinert werden kann, da diese wohl Objektivität und Quantifizierung garantieren können, ohne unvorhersehbare Ergebnisse zu liefern.

Introduction

The MN zonation scheme has been the main chronologic reference system for the Neogene land mammal faunas of Europe, and arguably most of Eurasia, since it was first proposed by MEIN (1975). It was quickly accepted by most European paleontologists (FAHLBUSCH 1976, 1991), being rooted in a European stratigraphic tradition based on the concept of reference faunas. This tradition reaches back to CUVIER (FAHLBUSCH 1991) and is dictated chiefly by the rare direct stratigraphic superposition of the vast majority of European, West Asian and North African fossil localities it attempts to chronologically order. Yet, the MN system has been the subject of ongoing debate ever since it was first proposed, and there seems to be little agreement about what, if anything, the MN units represent in relationship to formally recognized stratigraphic concepts (BRUIJN et al. 1992; FAHLBUSCH 1976, 1991; LINDSAY & TEDFORD 1989).

As originally codified by MEIN (1975), the MN units were characterized by three criteria: 1) formes caractéristiques de lignées évolutives (key species of evolving lineages); 2) associations (commonly associated taxa); 3) apparitions (common first appearances). Localities were chronologically ordered for 18 "zones" (0-17/Q1) into the following geographic blocks: 1) North Africa; 2) Spain and Portugal; 3) France; 4) Germany, Switzerland, Italy; 5) Austria, Hungary, Czechoslovakia, Poland; 6) Rumania, U.S.S.R; 7) Yugoslavia, Greece, Turkey (MEIN 1975: table 1). MEIN (1979) retained essentially the same system, providing some useful updates to it. BERNOR (1978, 1983, 1984) and BERNOR & PAVLAKIS (1987) analyzed the biogeographic relationships of several Eurasian and African late Miocene faunas and reported distinct patterns of biogeographic provinciality. MEIN's (1989) revision was a major one in that he eliminated MN "zone 0" and implemented a provincial organization of Neogene faunas recognizing the following geographic blocks: 1) W. Europe; 2) C. Europe; 3) E. Europe; 4) S. E. Europe; 5) W. Asia; 6) N. Africa. In addition, MEIN (1989) characterized his faunas by: 1) Common Taxa (W+C Europe and Other); 2) First Appearance (W+C Europe and Other); 3) Last Occurrence (W+C Europe and Other). Significant here was the elimination of the „formes caractéristiques de lignées évolutives“ found in the 1975 scheme and the addition of a listing of the reference faunas for each unit. This revision brought much clarity to the system and has been set as its empirical foundation.

There has been a considerable parallel effort to MEIN's to develop a chronology of MN "zones". DAAMS & FREUDENTHAL (1981) openly challenged the utility of MN "zones", arguing that they lacked a biostratigraphic basis, and as such often suffered from errant correlations. STEININGER et al. (1989) made a concerted effort to identify independent chronologic tie points to MN "zones", based on marine interdigitations and both magnetostratigraphic and radioisotopic correlations. This effort was expanded through the 1992 Schloss Reinsburg conference which FAHLBUSCH co-organized (BERNOR et al. 1996c). The conference provided several new chronologic correlations, including: RÖGL & DAXNER-HÖCK's (1996) Central-Eastern Paratethys correlations, STEININGER et al.'s (1996) revision of Western Eurasian and N. African chronologic tie points, SEN's (1996) report on new European magnetostratigraphic correlations, recent magnetostratigraphic correlations at Sinap, Turkey (KAPPELMAN et al. 1996; LUNKKA et al. in press), and single crystal A^{40} / Ar^{39} radioisotopic ages for several Western Eurasian localities (BERNOR et al. 1996d; SWISHER 1996; WOODBURNE et al. 1996). There were

further reports on Spain's emerging magnetostratigraphic correlation of Miocene age localities (GARCÉS et al. 1996; KRIJGSMAN et al. 1996)

FAHLBUSCH (1991:162) concluded that MN units should not be given the character of biozones in a formal biostratigraphic sense, but emphasized the importance of retaining MEIN's reference faunas to characterize MN units. BRUIJN et al. (1992) reached a similar conclusion, recommending maintenance of the reference fauna system for characterizing individual MN units, but emphasizing stage-in-evolution as the true foundation of the MN system.

Despite the continuing controversy over the formal nature of the MN system, there can be no doubt that it has been, and continues, to be useful for comparing faunas far distant from the Central and Western European reference faunas (Table 1). The use of well calibrated stratigraphic sequences with good faunal expression has been emphasized in the last 20 years and is yielding refined chronologic resolution and new insights into the biogeographic relationships of Western Eurasian Neogene mammal faunas. That contradictions occur between different workers on the MN attribution of specific faunas, and that localities previously referred to a particular MN unit are now found to chronologically correlate with another MN unit is not only expected, but constructive for the ongoing revision of the system. This does not detract from the value of MEIN's zonation, but rather underlines its great value as a correlation tool. In fact, if asked, European colleagues will usually state that while the system has many flaws

Table 1: MN unit reference localities: assigned and predicted unit referrals.

REFERENCE LOCALITY*	MN UNIT	PREDICTED
St. Vallier	17	17
Triversa	16	16
Arondelli	16	16
Perpignan	15	15
Podlesice	14	14
El Arquillo 1	13	13
Los Mansuetos	12	12
Crevillente-3	11	11
Masia del Barbo	10	10
Can Llobateres	9	8
Anwil	8	7
Steinheim	7	6
Sansan	6	6
Pont Levoy	5	5
La Romieu	4	5
Wintershof-West	3	NO DATA AVAILABLE
Laugnac	2b	NO DATA AVAILABLE
Montaigu-le-Blin	2a	5
Paulhiac	1	NO DATA AVAILABLE

*Note: Reference Localities follow Mein, 1989

and uncertainties, it is the only one that actually works in the absence of absolute chronologic control, a point particularly emphasized by BRUIJN et al. (1992). Stability is also commonly invoked as a reason for using the MN system, and FAHLBUSCH (1991) has made a strong and thoughtfully reasoned plea to avoid changing its definitions, even when such changes might seem to offer apparent improvements. Thus, there appears to exist a peculiar mismatch between the agonized and defensive love-hate attitude of many European workers to the MN system, and the relative ease with which localities are assigned to MN units by these same workers. In principle, this could mean either that the formal difficulties are less important than they appear, or that the apparent success of the MN system is, in fact, only the result of a grand delusion.

Meanwhile, another opportunity to address the performance of the MN system purely as a biochronological framework has become available in the form of the appearance event ordination (AEO) technique (ALROY 1994). In this paper we apply a simpler version of AEO, called disjunct distribution ordination (DDO; ALROY 1992), to a set of Western Eurasian Neogene to Quaternary mammal localities derived from the NOW database (FORTELIUS et al. 1996). Our goal at this stage is not to revise the MN system *per se*, but to address a few simple and commonly raised questions. For example: How does the MN system perform by the standards of an independent, algorithm-driven test such as AEO or DDO? Can the MN system be successfully applied outside Western and Central Europe? We wish to take advantage of the fact that the DDO routine provides a neutral, independent, and explicit means of ordering localities based only on their faunal lists: i. e., it performs exactly the same function as the MN system, but without any subjective element involving external information or prejudice. The DDO technique also has been used by AZANZA et al. (1997) for a similar purpose, although they employed a smaller database of strictly western Mediterranean localities.

Our analysis is simple and preliminary, and we do not claim to have definitive answers. This is especially true since we have made no attempt to use external temporal controls such as radioisotopic dates or stratigraphy. We will, however, argue that our results suggest a strong vindication of the MN system as redefined by FAHLBUSCH (1991), especially in its emphasis on whole reference faunas as its basis. We also shall argue that the MN system is potentially useful for continental-scale correlation, despite the small number of taxa with such extensive distributions.

Material and Methods

Material

The data used for this study derive from the NOW (Neogene of the Old World) database, originally the result of a concerted effort to revise the systematic and stratigraphic data for fossil land mammal localities of Central Europe and the Eastern Mediterranean belonging to the time interval of 15 - 5 Ma (BERNOR et al. 1996a, c; FORTELIUS et al. 1996). It has since been expanded to include Western Europe, the Black Sea region, and the parts of Central Asia that have been worked by scientists from the former Soviet Union, as well as both older and younger localities. The database is being continuously revised by the members of the NOW Advisory Board, and data sets may be requested from MF or from gem_dig@gaia.pc.helsinki.fi. The data sets used for the analyses reported here are also available from JA.

Methods

Biochronological schemes are based either intuitively or explicitly upon three major sources of data: similarities among taxonomic assemblages of geographically associated faunas,



Figure 1: Geographic distribution of localities used in the analyses presented herein. Some localities east of Turkey and the Black Sea are not shown in this figure.

superposition of localities within stratigraphic sections, and independent (usually magnetostratigraphic or radioisotopic) geochronologic age estimates. Appearance event ordination seeks to integrate as much of this information as possible (ALROY 1992, 1994). The first two sources of data can be formalized by inferring first/last, or "F/L," statements. The F/L statements are used to constrain a relative sequence of first and last appearance events (FAEs and LAEs) that is derived by multivariate ordination. Geochronologic data may be used to calibrate the resulting sequence. A method of integrating paleomagnetic stratigraphy by using it to constrain the sequence is in development but has not yet been implemented.

An F/L statement is the observation that the FAE of one taxon predates the LAE of another. Such observations are not trivial, because it is logically possible for all the taxa in a data set to have age ranges that are completely "disjunct," or non-overlapping. In such a situation, half of all possible F/L statements would be demonstrable, but the other half would not. A sufficiently large set of F/L statements should demonstrate not just the trivial relationships in the first category, but the non-trivial statements that imply overlaps of age ranges (i.e., "conjunctions").

F/L statements offer several methodological advantages: 1) both faunal associations and biostratigraphic relations can be expressed as F/L statements - an F/L statement involving two taxa i and j can be inferred either if i and j occur in the same taxonomic assemblage, or if i is found beneath j in a stratigraphic section; 2) because of this, the method of computing F/L statements makes use of all taxonomic lists and biostratigraphic sections, incomplete or not; 3) very large numbers of F/L statements are generated by large taxonomic lists (the "Rosetta Stone" property); 4) because demonstrated F/L statements cannot be disproved by further data, the "true" set of all F/L statements is inexorably approached as more and more data are collected ("convergence"); 5) a full set of F/L statements would immediately imply a perfectly accurate relative ordering of FAEs and LAEs, which would be exactly equivalent to a relative age-range chart; and 6) no other sorts of relationships among events, such as LAEs coming before FAEs in stratigraphic sections, have even a majority of these properties; nor do the raw presence-absence data presented by taxonomic lists.

The problem solved by AEO is that the matrix of all F/L statements is, in practice, often far from complete. Therefore, inferring the "true" appearance event sequence (i.e., the true age range chart) is not a trivial matter. The method proceeds on the assumption that the best inferred sequence is the one that implies the smallest number of F/L relationships that thus far have not been directly proven. This criterion of parsimony is exactly equivalent to saying that the best age range chart implies the fewest overlaps of age ranges. A primary appearance event sequence is computed by means of an algorithm related to correspondence analysis; this initial hypothesis is "optimized" by swapping neighboring events in the sequence to break up overlaps of age ranges. Details are given elsewhere (ALROY 1992, 1994, 1996). Because the current data set is preliminary and the current analysis is exploratory, we will take a minimalistic approach to analyzing the data.

We will not employ stratigraphic data to infer F/L statements, which means that we will use the simpler DDO algorithm instead of the more complex AEO algorithm (DDO assumes that all F/L statements derive from examination of taxonomic assemblages). We will not use geochronologic data to calibrate the resulting event sequence. We will not use surviving taxa to "polarize" the ordination and eliminate the bogus "last appearances" of these taxa from the sequence. Finally, we will not make any effort to control for conflating biogeographic signals in the data, even though an algorithm to do just this is available (the "square graph" method: ALROY 1996). Thus, we are making it possible for strong patterns of diachrony among geographic regions to surface in the analysis, if that turns out to be parsimonious.

Once the ordination has been performed, the output needs to be interpreted by translating the relative sequence of taxonomic appearances, which by convention is numbered consecutively from oldest to youngest, into a relative sequence of faunal assemblages. This is because we will seek to evaluate the MN system by referring to MN assignments for particular localities. Importantly, the ordination does not directly assign localities to any one "point" in time because it operates only on a matrix of F/L statements involving relationships between pairs of taxa, and generates an appearance event sequence that involves only these taxa - localities per se do not enter into the computations. The sequence of localities is therefore a secondary consideration. It is dealt with by computing a "concurrent range zone" for each taxonomic list, which is just the narrowest range of events across the sequence that spans the range zones of all taxa found in the list.

For example, suppose that a list includes three taxa x , y , and z , and that their age ranges across the sequence are 846 - 932 (FAE - LAE of x), 903 - 908 (y), and 897 - 906 (z). The concurrent range zone is 903 (FAE of y) to 906 (LAE of z). Note that the age range of x was not useful in this computation because it completely exceeded those of the other taxa. Because we want to correlate the range zones against the MN assignments, we will take the further step of using the

midpoint of the range zone instead of both of the event numbers that specify it: so in this case the locality will be assigned to event 904.5. Because we have not yet used stratigraphic or geochronologic data to temporally “polarize” the ordination results, from this point on we will use the more agnostic term “edge sequence” (which has no necessary temporal connotation) instead of “event sequence.” The concurrent range zones of taxonomic lists then refer to their positions in the edge sequence, or “edge positions”.

Results

In this section we will discuss three simple analyses of the ordination output. First, we will show that the ordination’s relative arrangement of faunal lists is largely the same as the traditional arrangement implied by MN unit assignments. Second, we will show that the same relationship holds regardless of the taxonomic level of the analysis (genus, species, or combined), and regardless of the geographic scope of the analysis (Western Europe, Eastern Europe/Central Eurasia, or combined; Figure 1). Surprisingly, the relationship is actually strengthened by combining data sets. Thus, there is no evidence that, say, dubious species-level

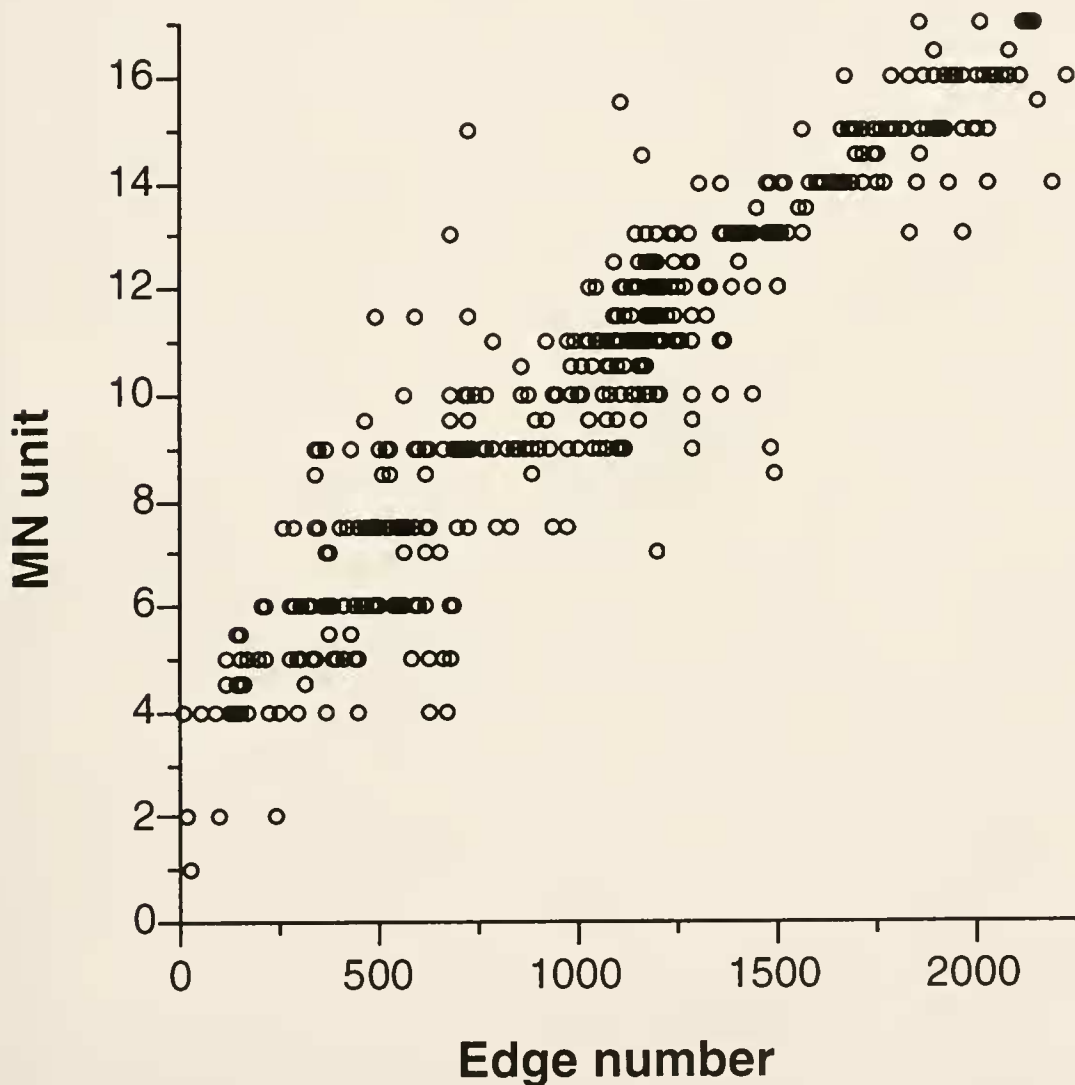


Figure 2: Correlation between concurrent edge positions and MN unit assignments of faunal lists. Edge numbers are based on a disjunct distribution ordination of the 654 lists in the combined data set. The ordination and the zone assignments reflect the same underlying temporal gradient.

data or geographically remote localities “corrupt” the data set’s biochronological signal. Third, we will show that deviations from this relationship are similar in the two geographic subsets of the data, and are less severe for well-known faunas. In fact, just a half-dozen identifications appear to be enough to place any faunal assemblage firmly within the ordination.

Ordination vs. MN units

We will begin by discussing a combined analysis of all 654 of the faunal lists in the data set. Here, each genus is treated as a different taxon than the species it includes, and all of the genera and species are put into the data matrix at once. This very unorthodox, “hybrid” method of analysis has been shown to work well with similar data sets (ALROY 1996). A total of 796 genera and 1829 species are present in the lists, but for the purpose of ordination this set was trimmed by removing “singletons”. Singletons are taxa that yield no particular information about the relative age of faunal assemblages because they are found only in a single faunal list. Ranges of singletons across the sequence were computed after the ordination by “plugging them in” to the edge positions occupied by their respective faunal lists. The resulting ordination involved 1490 non-singleton taxa and therefore included 2980 edges. The simplest way to illustrate the correspondence between this hypothesized edge sequence and the traditional MN zonation is to plot the MN assignments of the localities against their edge positions (Figure 2; 131 of the 654 lists are excluded because they do not have MN unit assignments). There is a clear, monotonic relationship that is essentially linear. It makes no great difference if a correlation is computed on the raw data, which yields a Pearson’s r coefficient of 0.933, or on the same data after performing a rank transformation, which yields a Spearman’s r coefficient of 0.925. It is self-evident that both measures are responding to the same underlying signal. Because we have not employed stratigraphic, biogeographic, or geochronologic data, or even taken note of which taxa are extinct and which are extant, we can infer that this signal is entirely faunistic, resulting from the replacement of taxa as expressed by shifting patterns of faunal association. These patterns clearly are being captured by the conjunctive information expressed in the F/L statements.

Combined vs. Subdivided Data Sets

The original faunal set was not specifically gathered for statistical analysis. Yet, quite surprisingly, it yields a strong statistical signal, and therefore it is natural to ask if subdividing the data might improve the ordination. Specifically, we will test two hypotheses: that genera might be more reliable than species because they are more taxonomically stable, temporally long-ranging, and geographically widespread; and, that a pure data set of faunas from the “West” region might be more reliable because these data have fewer taxonomic problems and should include fewer conflating biogeographic patterns.

In fact, separate analyses at the genus and species levels do not improve the ordination (Figure 3). A genus level run that included the same 523 faunal lists yielded a slightly weaker relationship between MN assignments and edge positions (Spearman’s $r = 0.909$; Pearson’s $r = 0.904$). Counter to this hypothesis, the species data performed even better (Spearman’s $r = 0.939$; Pearson’s $r = 0.935$), although these figures are essentially indistinguishable from those yielded by the combined data set analysis.

Splitting the data set geographically also fails to improve the results (Figure 4). By itself, the East data set performs very poorly (Spearman’s $r = 0.804$; Pearson’s $r = 0.677$). The very worst problem is with Aliveri, a diverse fauna that nonetheless falls as an extreme outlier in Fig. 4. Its conventional MN unit assignment implies that it should have fallen at a much lower edge position than it did. Intuitively, one would think to attribute the poor result for the East both to the small number of lists in the subset, and to the poor representation of the Early Miocene

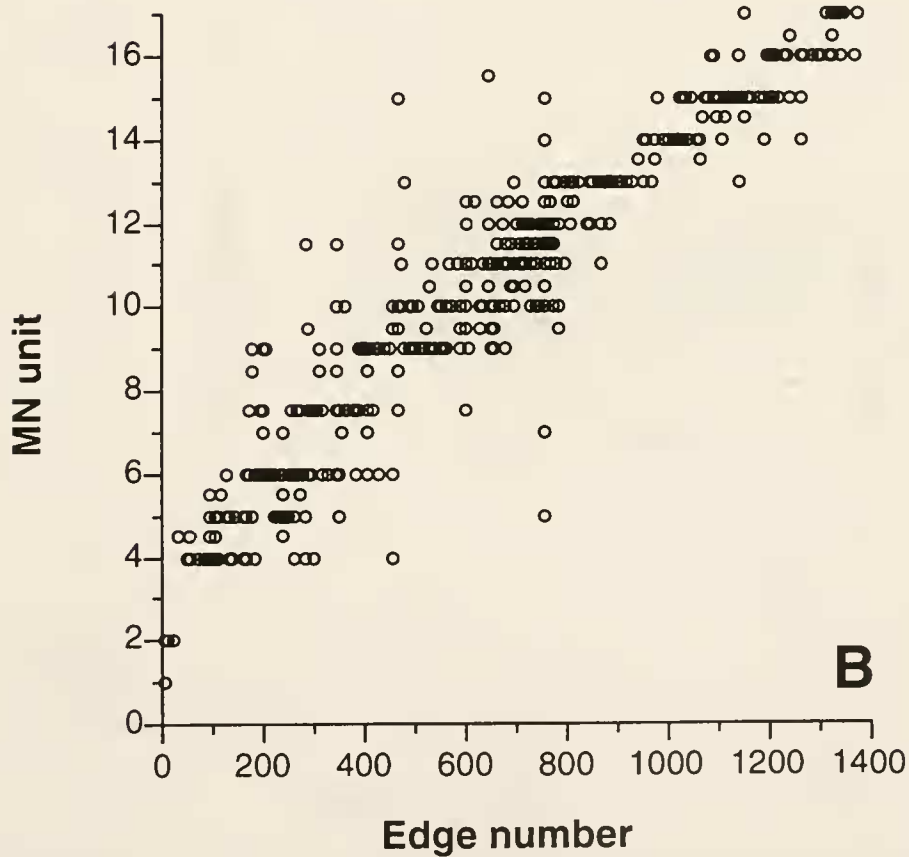
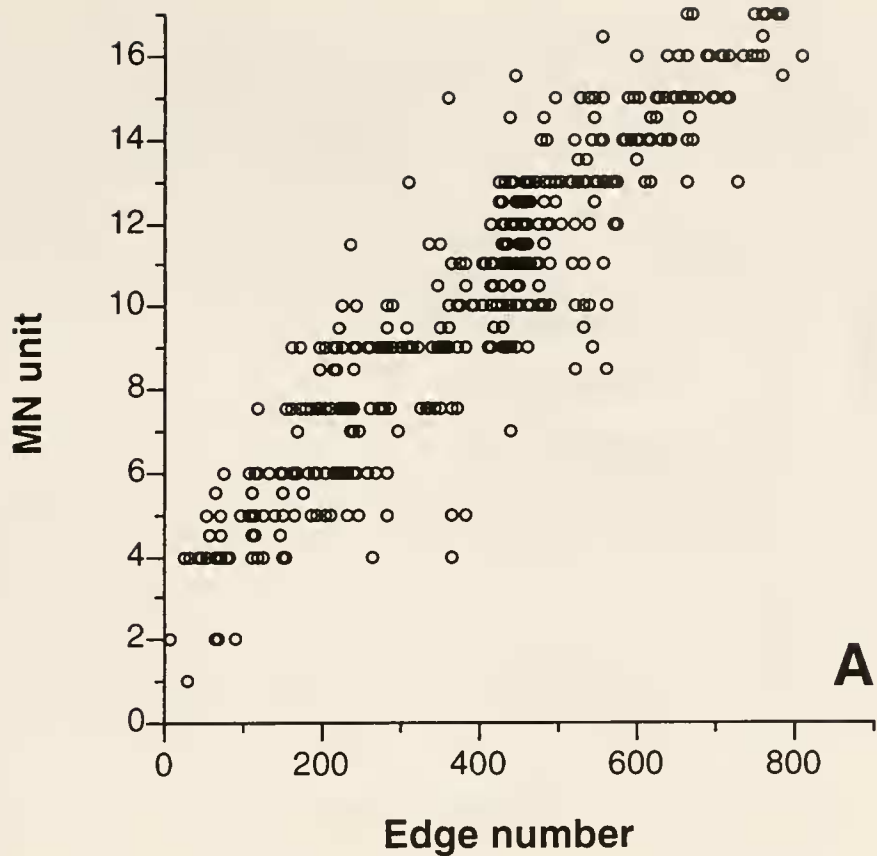


Figure 3: Correlations between concurrent edge positions and MN unit assignments produced by separate analyses of genera and species. Each point is a faunal list. Each taxonomic subset analysis produces a poorer relationship than does the combined data set (Fig. 2). A) Correlation based on a genus-level analysis. B) Correlation based on a species-level analysis.

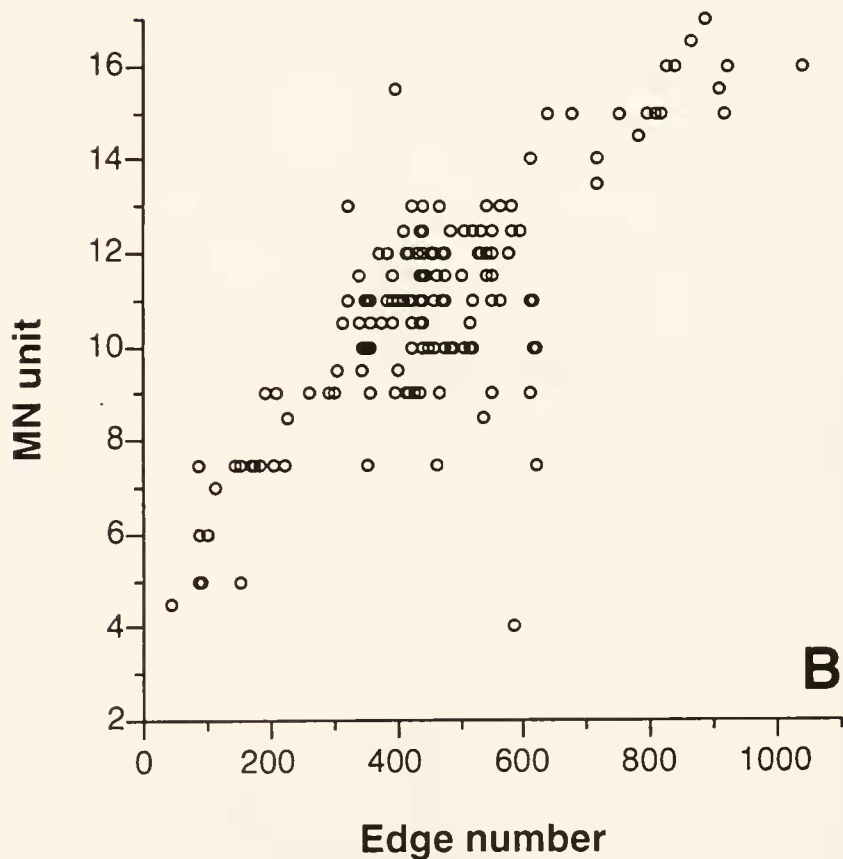
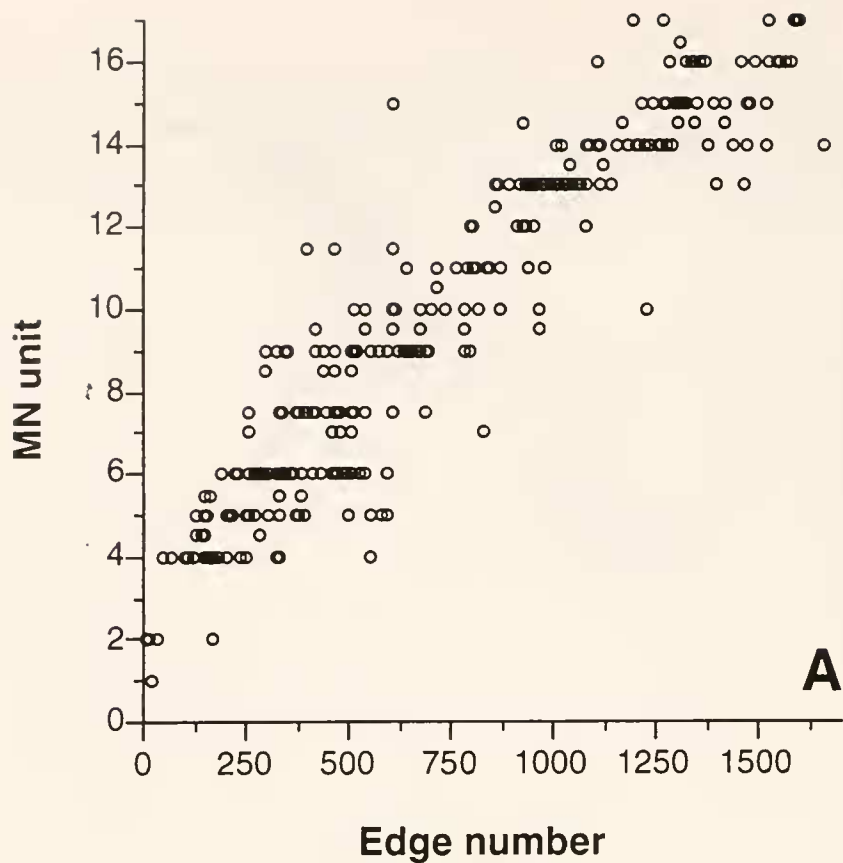


Figure 4: Correlations between concurrent edge positions and MN unit assignments produced by separate analyses of the West and East data sets. Each geographical subset analysis produces a poorer relationship than does the combined data set (Fig. 2). A) Correlation for 345 lists analyzed in the West run. B) Correlation for 178 lists analyzed in the East run. Many of the East lists did not have MN assignments. Outlier at edge 585.5 and MN unit 4 is Aliveri.

in this subset, which makes the temporal gradient shorter and therefore harder to perceive. However, data for the East lists from the combined run demonstrate a substantially stronger MN unit/edge position relationship (Spearman's $r = 0.868$). Therefore, we cannot attribute the poor performance of the separate East run to these factors alone: it must be the case that the temporal position of these lists has been informed by the composition of the West lists, which could only be the case if conjunctions between taxa seen only in the West also were relevant to the East. In other words, the West data must be "patching" important gaps in the conjunctural pattern that applies to cosmopolitan taxa.

MN Unit Predictions vs. List Length

Not all of the faunal lists occupy a predictable location in the edge sequence. In fact, if one computes residual MN unit values based on the relationship seen in Fig. 2, one discovers that they average 0.92 MN units, and have a standard deviation of 1.33. Thus, the predicted and assumed unit numbers are often quite different. Most of this "noise," however, is due to an entirely predictable phenomenon: when faunal lists include very few taxa, it is difficult to correlate them precisely. So it comes as no surprise that these residual values decline as the number of taxa (genera plus species) in a list increases (Figure 5). The rank-order correlation

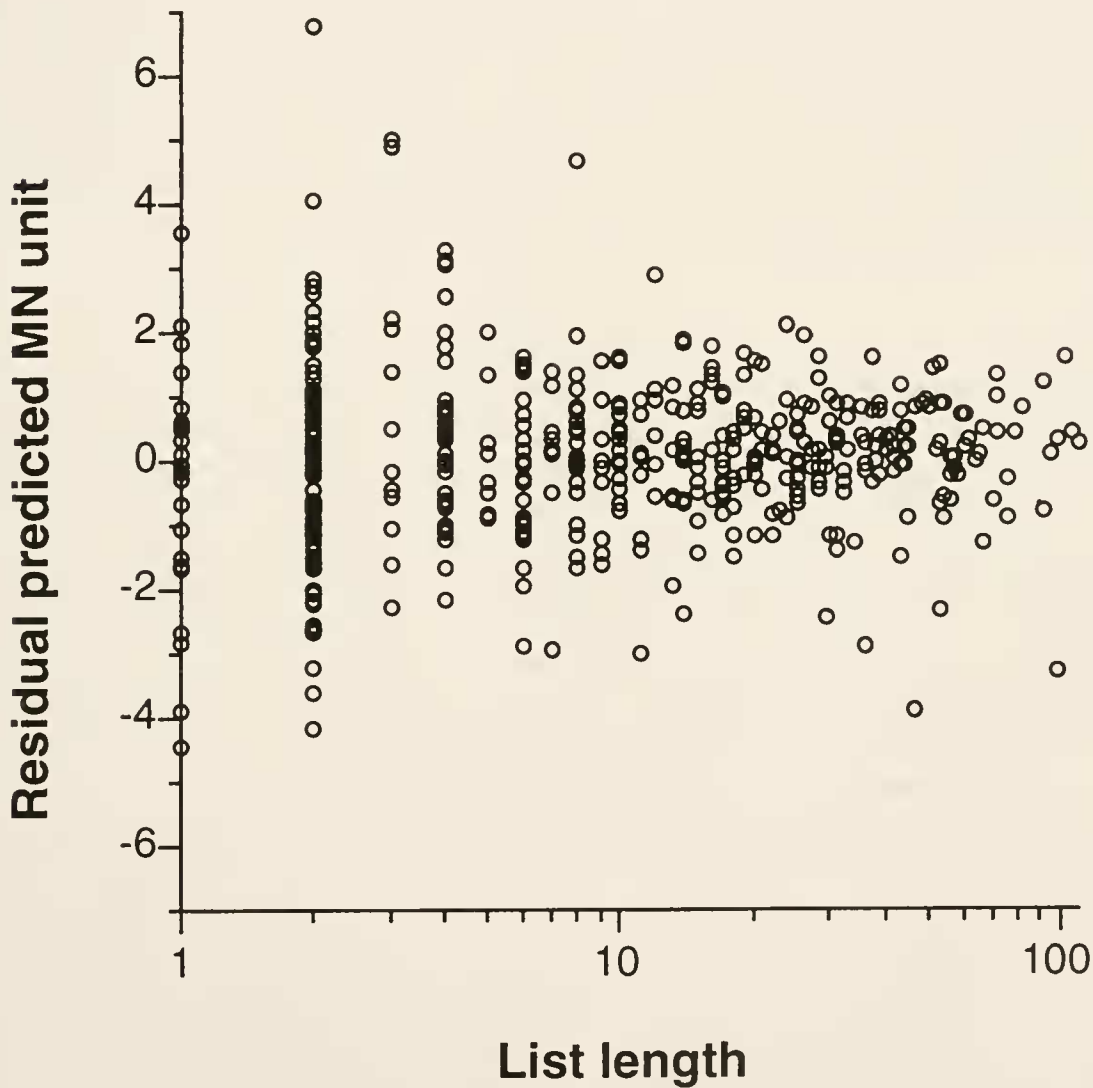


Figure 5: Residual predicted MN unit assignments and list lengths. Longer lists show smaller residuals. Residuals are based on a least-squares fit to the relationship shown in Fig. 2. List lengths are equal to the sum of the number of genera plus species in each list.

between the absolute value of these residuals and the combined taxon counts is -0.235 ($p < 0.001$).

Visually, it appears that including at least 20 taxa almost always guarantees a correlation “error” of two MN units or less. Only six of the 146 lists that include this many taxa exceed this limit: Aliveri (MN 4 vs. „predicted“ MN 7.9 [=MN 8]), Massendorf (5 vs. 7.9 [=MN 8]), Montaigu-le-Blin (2 vs. 5.3 [=MN 5]), Puttenham (5 vs. 7.4 [=MN 7]), Simorre (7/8 vs. 5.4 [=MN 5]), and Ulm-Westtangente (2 vs. 4.4 [=MN 4]). Most of these lists cluster close to the beginning of the edge sequence. Not coincidentally, MN units 1 through 3 are poorly represented in the current data set, with just 1, 5, and 0 lists, respectively. There is no reason to expect the ordination to perform well for an interval this poorly sampled. Furthermore, this undersampling resulted in the predicted MN unit at edge 0 being not 0 but 3.8, so all of the lists in the current analysis must have a predicted MN unit of at least this much.

Apart from undersampling, another important factor is the widely-known statistical difficulty of correctly ordering data close to the end of a gradient, which is known as the “arch effect” in the ecological literature (GAUCH 1982). Essentially, points at the ends of gradients “collapse” into an uninterpretable clump. Based on this, we would expect *a priori* that the ordination would be maximally unreliable near the extremes of the temporal gradient.

It also is important to note that the ordination does perform very well for the large majority of the localities, as shown by an examination of the reference localities that we were able to include in the analysis (Table 1). With the exceptions of Montaigu-le-Blin and Arondelli, all of these localities are in the “right” order, and most of them have predicted MN unit numbers that are very similar to the predetermined values. An interesting aspect of this analysis is that MEIN’s (1989) reference faunas for MN 7 (Steinheim) and MN 8 (Anwil) performed well (Steinheim = 6.3, or MN 6; Anwil = 7.2, or MN 7), whereas the recommended reference fauna for MN 7+8, La Grive St. Alban, performed relatively poorly (5.9 = MN 6).

Discussion

The main result of the DDO analysis is a strong correlation between MN assignment and edge position. In other words, both methods successfully extract the biochronologic signal from the faunal lists, an interpretation supported by the result that the mean error of MN unit assignment relative to edge position decreases as faunal lists grow longer (Fig. 5). A similar result was reported by AZANZA et al. (1997), who showed that geochronological age estimates also correlate strongly with edge positions. Importantly, the correlation between MN assignment and edge position is highest for the combined data set, showing that the inclusion of an area outside the type region of the MN system does not dilute the signal but instead strengthens it. This is a highly significant result, especially because the East data set shows a much weaker pattern when analyzed by itself. It suggests that a continental scale application of the MN system is not only possible, but in fact preferable to a regional one.

The result that the combined East-West data set shows the highest correlation may appear counterintuitive, especially given the fact that most of the taxa involved have relatively restricted geographic ranges, and that the number of taxa with continental-wide distribution is limited, even when taxonomic artifacts are taken into account. For the DDO analysis the explanation is straightforward. Since the analysis is based on conjunctions, limited geographic distribution of individual taxa is not a problem as long as the distribution of some taxa allows successive carry-over of ties between adjacent regions. The fact that faunas in distant regions may share no taxa therefore does not, as such, exclude those faunas from DDO.

We would like to suggest that the discomfort often expressed about the formal aspects of the MN system reflects a fundamental dilemma: in actual practice the system has been developed

in an intuitive manner closely analogous to DDO, i. e., by applying a criterion of parsimony to all of the available evidence; but the stated definitions involve a smaller number of “important” taxa that are often missing from the faunal lists. Whether this is true or not, the fact remains that the system could be treated in this way, and that such usage could be formalized in terms of conjunction-based parsimony criteria. In other words, DDO analysis could eventually form an independent and potentially more rigorous framework for the MN system, and it is not fundamentally in conflict with present usage. This historical and intuitive continuity is an aspect of DDO that we feel should be strongly emphasized. Other workers have come to similar conclusions after employing this method independently (e.g., AZANZA et al. 1997).

It is clear from our analysis that DDO produces occasional edge position values that disagree strongly with conventional MN assignments. This can have many reasons, the most common of which is that there is an inadequate number of conjunctions demonstrated by a faunal list because it is very short. A secondary problem is that when a locality is at one end of the age spectrum, the “older” taxa in the list may fail to provide a strong temporal signal and the list may be “folded” too deeply into the edge sequence. These warning signs can be recognized easily, leaving just a few localities where the discrepancy is worth investigating (e. g., Aliveri). We suspect that DDO will be useful in this way for drawing attention to misidentified taxa, poorly supported age assignments, and highly unusual faunal assemblages that are hard to correlate, or, alternatively, to particularly good biochronologic marker taxa (if it can be shown that the DDO result is in error).

Using DDO also will allow for a formal extension of the MN system east of western Eurasia, into China. It has already been applied to Chinese faunas with some apparent success (e. g., QIU 1989). This success is to a large extent due to conjunction chains in which faunas from the East serve as „stepping stone faunas“ with ties to both ends of the chain. Thus, while Chinese faunas have few species-level taxa in common with Western Europe, they can still be assigned to an MN unit by our methods, due to their sharing species with faunas of Western Asia that in turn share other species directly with Western Europe, or indirectly through yet another intermediate in Eastern Europe. The further synonymization of Chinese taxa with more westerly ones and phylogenetic reconstruction of lineages common to China, West Asia and Europe will provide further bases for establishing East-West conjunctions.

It follows from the preceding discussion that restricting the basis for correlation to individual key lineages is more likely to impair than to improve its precision. There are several reasons for this, the first being the simple paucity of suitable taxa with sufficiently wide geographic distributions. Using only taxa with wide ranges also potentially aggravates problems of diachrony, since the dispersion of individual taxa across Eurasia is known to exhibit varying diachrony, even with the coarse scale of the MN system. In fact, such instances are mostly known because they appear diachronous even within the MN system (FORTELIUS et al. 1996), thereby showing that the system as used is not at the mercy of individual taxa.

The fact that the MN assignments of East and West localities exhibit no systematic difference relative to the DDO edge positions supports the conclusion that both methods use the same fundamental signal to rank the localities. Both systems may still be time-transgressive, of course, but this can only be judged on the basis of chronostratigraphic ties, and lies beyond our analysis here.

We must emphasize that we reject regionally restricted MN zonations as a means of improving the AEO or DDO analysis: clearly a larger Eurasian data set performs better. However, we are in no way arguing against developing local biostratigraphies or regional geochronologic frameworks that include independent geochronologic control. On the contrary, we strongly agree that the refinement of local sequences with demonstrable stratigraphic

superposition and ties to independent chronologies, such as magnetostratigraphy and marine zonations, constitutes one of the main directions that should be followed.

In the context of the present discussion we would like to emphasize another very important main direction for improving MN correlation: systematic revision on a continental scale. It seems likely that the main source of noise in present biochronologies is poorly resolved taxonomy and unrecognized synonymy. Following a general reorganization of taxonomic issues, the next important step is lineage reconstruction, because this will allow identification of those evolutionary lineages that actually perform the task of conjunction across geographic provinces. Large paraphyletic taxa like "Hipparion" (s.l.) have been recently segregated into multiple species lineages, providing a more resolved basis for correlation (BERNOR et al. 1989).

If the systematic foundation is the same everywhere over the entire study area, true stage-of-evolution data can be obtained from the faunas and used to establish a robust biochronologic system common to the entire area. One of the main hindrances to this goal lies in the inheritance of local, and long unrevised taxonomies, which create difficulties in establishing broader chronologic schemes such as the MN system.

Conclusions

The use of MN reference faunas is theoretically justified and in no way conflicts with the use of stage-of-evolution information. The "Meaning of MN-Zonation" in the sense of FAHLBUSCH is strongly supported. The MN system, and the systematic and geochronologic refinements that it continues to undergo, can be maintained in parallel with the emerging use of DDO and eventually AEO, which will bring a highly desirable element of objectiveness but is not expected to produce conflicting results. In fact, we expect these methods to eventually become a powerful means of evaluating the correlation of geographically widely separated localities to a common, Eurasian MN system.

Acknowledgements

We dedicate this paper to Professor Dr. Volker Fahlbusch on the occasion of his sixty-fifth birthday in acknowledgement of his important contributions to Eurasian vertebrate paleontology and the understanding of MN unit method and theory. Through his individual research contributions, as well as his skill in organizing and publishing major research volumes, he has effected major advances in this field. He has further offered considerable quiet support to many colleagues who have frequented the Bayerisches Institut für Paläontologie und Historische Geologie to study collections, collaborate on research projects, and otherwise obtain his scientific advice. We would especially like to acknowledge his direct contribution to the 1992 Schloss Reisenburg Workshop that formed the basis of the NOW database that we have used for our analyses herein. The Schloss Reisenburg Workshop was funded by the Volkswagen Stiftung and the creation of the database was funded by the Academy of Finland. We would like to thank the NOW advisory board for their continuing updates and revisions of the NOW database. JA would like to thank the Evolution of Terrestrial Ecosystems program at the Smithsonian Institution for supporting this research. RB would like to thank the Alexander von Humboldt Stiftung for two years sabbatical support of his work in Karlsruhe. MF would like to thank the European Science Foundation for financially supporting the NOW database through the Network on Hominoid Evolution and Environmental Change in the Neogene of Europe (HOMINET) and the Academy of Finland project no. 34080 for financial support. LW acknowledges financial support from the Swedish Natural Science Research Council.

References

- ALROY, J. 1992. Conjunction among taxonomic distributions and the Miocene mammalian biochronology of the Great Plains. - *Paleobiology* 18: 326-343, Lawrence.
- ALROY, J. 1994. Appearance event ordination: a new biochronologic method. - *Paleobiology* 20: 191-207, Lawrence.
- ALROY, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. - *Palaeogeography Palaeoclimatology Palaeoecology* 127: 285-311, Amsterdam.
- AZANZA, B., ALBERDI, M.T., CERDEÑO, E. & PRADO, J.L. 1997. Biochronology from latest Miocene to Middle Pleistocene in the western Mediterranean area. A multivariate approach. - pp. 567-574 in: AGUILAR, J.-P., LEGENDRE, S. & MICHAUX, J. (eds.), Actes du Congrès BiochroM'97. - Mémoires et Travaux de l'Institut de Montpellier de l'École Pratique des Hautes Études 21, Montpellier.
- BERNOR, R.L. 1978. The Mammalian Systematics, Biostratigraphy and Biochronology of Maragheh and Its Importance for Understanding Late Miocene Hominoid Zoogeography and Evolution. - Ph.D. diss., University of California, Los Angeles, 1-314, Los Angeles.
- BERNOR, R.L. 1983. Geochronology and zoogeographic relationships of Miocene Hominoidea. - pp. 21-64 in: CIOCHON, R.L. & CORRUCINI, R.S. (eds.), New Interpretations of Ape and Human Ancestry. - Plenum Press, New York.
- BERNOR, R.L. 1984. A zoogeographic theater and biochronologic play: The time-biofacies phenomena of Eurasian and African Miocene mammal provinces. - *Paléobiologie Continentale* 14: 121-142, Montpellier.
- BERNOR, R.L., FAHLBUSCH, V., ANDREWS, P., BRUIJN, H. DE, FORTELIUS, M., RÖGL, F., STEININGER, F.F. & WERDELIN, L. 1996a. The Evolution of Western Eurasian Neogene Mammal Faunas: A chronologic, systematic, biogeographic and palaeoenvironmental synthesis - pp. 449-470 in: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.), The Evolution of Western Eurasian Neogene Mammal Faunas. - Columbia University Press, New York.
- BERNOR, R.L., FAHLBUSCH, V., MITTMANN, H.-W. & RIETSCHEL, S. 1996b. The evolution of Western Eurasian Neogene Mammal Faunas: The 1992 Schloss Reinsburg Concept. - pp. 1-6 in: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.), The Evolution of Western Eurasian Neogene Mammal Faunas. - Columbia University Press, New York.
- BERNOR, R.L. & PAVLAKIS, P.P. 1987. Zoogeographic relationships of the Sahabi large mammal fauna (early Pliocene, Libya). - pp. 233-254 in: BOAZ, N.T., EL-ARNAUTI, A., GAZIRY, A.W., HEINZELIN, J. DE & BOAZ, D.D. (eds.), Neogene Paleontology and Geology of Sahabi. - Alan Liss, New York.
- BERNOR, R.L., SOLOUNIAS, N., SWISHER, C.C. III & VAN COUVERING, J.A. 1996c. The correlation of three classical "Pikermian" Mammal Faunas - Maragheh, Samos and Pikermi - with the European MN unit system. - pp. 137-156 in: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.), The Evolution of Western Eurasian Neogene Mammal Faunas. - Columbia University Press, New York.
- BERNOR, R.L., TOBIEN, H. & WOODBURNE, M.O. 1989. Patterns of Old World Hipparionine evolutionary diversification. - pp. 263-320 In: LINDSAY, E.H., FAHLBUSCH, V. & MEIN, P. (eds.), European Neogene Mammal Chronology. - Plenum Press, New York.
- BRUIJN, H. DE, DAAMS, R., DAXNER-HÖCK, G., FAHLBUSCH, V., GINSBURG, L., MEIN, P. & MORALES, J. 1992. Report of the RCMNS working group on fossil mammals, Reinsburg 1990. - *Newsletters on Stratigraphy* 26: 65-118, Stuttgart.
- DAAMS, R. & FREUDENTHAL, M. 1981. Aragonian: The stage concept versus Neogene mammal zones. *Scripta Geologica* 62: 1-17, Leiden.
- FAHLBUSCH, V. 1976. Report on the International Symposium on Mammalian Stratigraphy of the European Tertiary. - *Newsletters on Stratigraphy* 5: 160-167, Stuttgart.
- FAHLBUSCH, V. 1991. The meaning of MN zonation: Considerations for a subdivision of the European continental Tertiary using mammals. - *Newsletters on Stratigraphy* 24: 159-173, Stuttgart.
- FORTELIUS, M., WERDELIN, L., ANDREWS, P., BERNOR, R.L., GENTRY, A., HUMPHREY, L., MITTMANN, H.-W. & VIRANTA, S. 1996. Provinciality, diversity, turnover, and paleoecology in land mammal faunas of the later Miocene of Western Eurasia. - pp. 414-448 in: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.), The Evolution of Western Eurasian Neogene Mammal Faunas. - Columbia University Press, New York.

- GARCES, M., AGUSTI, J., CABRERA, L. & PARES, J.M. 1996. Magnetostratigraphy of the Vallesian (late Miocene) in the Vallés-Penedés Basin (northeast Spain). - *Earth and Planetary Science Letters* **142**: 381-396, Amsterdam.
- GAUCH, H.G. 1982. *Multivariate Analysis in Community Ecology*. Cambridge Studies in Ecology. - Cambridge University Press: Cambridge.
- KAPPELMAN, J., SEN, S., FORTELIUS, M., DUNCAN, A., ALPAGUT, B., CRABAUGH, J., GENTRY, A., LUNKKA, J.P., McDOWELL, F., SOLOUNIAS, N., VIRANTA, S. & WERDELIN, L. 1996. Chronology and biostratigraphy of the Miocene Sinap Formation of Central Turkey. - pp. 78-95 in: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. - Columbia University Press, New York.
- KRIJGSMAN, W., LANDEREIS, C.G., DAAMS, R. & VAN DER MEULEN, A.J. 1996. Magnetostratigraphic dating of the middle Miocene climate change in the continental deposits of the Aragonian type area in the Calatayud-Teruel Basin (Central Spain). *Earth and Planetary Science Letters* **142**: 367-380, Amsterdam.
- LINDSAY, E.H. & TEDFORD, R. 1989. Development and application of land mammal ages in North America and Europe, a comparison. - pp. 601-624 in: LINDSAY, E.H., FAHLBUSCH, V. & MEIN, P. (eds.), *European Neogene Mammal Chronology*. - Plenum Press, New York.
- LUNKKA, J.P., FORTELIUS, M., KAPPELMAN, J.W. & SEN, S. in press. Chronology and mammal faunas of the Miocene Sinap Formation, Turkey. - pp.00-00 in: AGUSTI, J. ANDREWS, P. & ROOK, L. (eds.), *European Science Foundation Network on Hominoid Evolution and Environmental Change in Europe, workshop proceedings volume*. - Cambridge University Press, Cambridge.
- MEIN, P. 1975. Résultats du Groupe de Travail des Vertébrés. - pp. 78-81 in: *Report on Activity of the RCMNS Working Groups (1971-75)*, Bratislava.
- MEIN, P. 1979. Rapport d'activité du groupe travail des vertébrés mise à jour de la biostratigraphie du Néogène basée sur les mammifères. *Annales Géologiques des Pays Helléniques* **3**: 1367-1372, Athens.
- MEIN, P. 1989. Updating of MN zones. - pp. 73-90 in: LINDSAY, E.H., FAHLBUSCH, V. & MEIN, P. (eds.), *European Neogene Mammal Chronology*. - Plenum Press, New York.
- QIU, Z. 1989. The Chinese Neogene Mammalian Biochronology - Its correlation with the European Neogene mammalian zonation. - pp. 527-556 in: LINDSAY, E.H., FAHLBUSCH, V. & MEIN, P. (eds.), *European Neogene Mammal Chronology*. - Plenum Press, New York.
- RÖGL, F. & DAXNER-HÖCK, G. 1996. Late Miocene Paratethys correlations. - pp. 47-55 in: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. - Columbia University Press, New York.
- SEN, S. 1996. Present state of magnetostratigraphic studies in the continental Neogene of Europe and Anatolia. - pp. 56-63 in: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. - Columbia University Press, New York.
- STEININGER, F.F., BERNOR, R.L. & FAHLBUSCH, V. 1989. European Neogene marine/continental chronologic correlations. - pp. 15-46 in: LINDSAY, E.H., FAHLBUSCH, V. & MEIN, P. (eds.), *European Neogene Mammal Chronology*. - Plenum Press, New York.
- STEININGER, F.F., BERGGREN, W.A., KENT, D.V., BERNOR, R.L., SEN, S. & AGUSTI, J. 1996. Circum-Mediterranean Neogene (Miocene and Pliocene) marine-continental correlations of European mammal units. - pp. 7-46 in: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. - Columbia University Press, New York.
- SWISHER, C.S. III. 1996. New $^{40}\text{Ar}/^{39}\text{Ar}$ dates and their contribution toward a revised chronology for the late Miocene nonmarine of Europe and West Asia. - pp. 64-77 in: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. - Columbia University Press, New York.
- WOODBURNE, M.O., BERNOR, R.L. & SWISHER, C.C. III. 1996. An appraisal of the stratigraphic and phylogenetic bases for the "Hipparion" Datum in the Old World. - pp. 124-136 in: BERNOR, R.L., FAHLBUSCH, V. & MITTMANN, H.-W. (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. - Columbia University Press, New York.